

# Habitat selection models to account for seasonal persistence in radio telemetry data

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**Abstract** Models for the analysis of habitat selection data incorporate covariates in an independent multinomial selections model (McCracken et al. 1998) Ramsey and Usner 2003 and an extension of that model to include a persistence parameter (2003). In both cases, all parameters are assumed to be fixed through time. Radio telemetry data collected for habitat selection studies typically consist of animal relocations through time, suggesting the need for an extension to these models. We use a Bayesian approach that allows for the habitat selection probabilities, persistence parameter, or both, to change with season. These extensions are particularly important when movement patterns are expected to differ seasonally and/or when availabilities of habitats change throughout the study period due to weather or migration. We implement and compare the models using radio telemetry data for westslope cutthroat trout in two streams in eastern Oregon.

**Keywords** Bayesian · Habitat association · Resource selection · Multinomial logit · Westslope cutthroat trout

## 1 Introduction

Radio telemetry is an important tool for investigating the movement and habitat use of animals over time. The data from radio telemetry studies typically consist of

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repeated measurements on individuals. In habitat selection studies, these data may be sequences of habitat types representing successive relocations of the tagged animals over time. That is, for animal  $i$ ,  $Y_i = (y_{i1}, y_{i2}, \dots, y_{ik})$ , where  $y_{ij}$  is the habitat type or class in which animal  $i$  is located at time  $j$ . Characteristics of the habitat may also be recorded for each sighting as continuous or discrete covariates. A goal of habitat association studies employing radio telemetry is to compare the frequencies with which different habitat types are visited and to identify possible habitat characteristics that might influence these frequencies. The relative frequencies should be compared to the relative availabilities of the habitat types to allow the researcher to draw conclusions as to the selection, or disproportionate use compared to availability, of resources (Johnson 1980).

McCracken et al. (1998) use an independent multinomial selections (IMS) model to analyze radio telemetry habitat data. Fitting the IMS model provides estimates of habitat selection probabilities (HSP) by means of a multinomial logit parameterization that incorporates habitat characteristic variables. Under the IMS model, relocations of an individual are assumed to be independent, the HSP are assumed to be identical for all individuals, and habitat selections for different individuals are assumed to be independent. Ramsey and Usner (2003) introduce a persistence model (PM) to relax the assumption of independent relocations. The PM, in addition to estimating HSP, estimates a persistence parameter,  $\eta$ , in which  $\eta = 1$  corresponds to the IMS model and  $\eta < 1$  indicates animals' tendency to persist in habitat classes.

We reformulate the PM as a Bayesian model and add model components that allow the HSP, the persistence parameter, or both to change with seasons. Thomas et al. (2004) provide a nice illustration of the use of Bayesian methods to estimate resource selection under the framework of the multinomial distribution. Our work further illustrates the flexibility of the Bayesian approach for tackling difficult problems while maintaining a simple method of constructing uncertainty intervals. We consider radio telemetry data collected on fish in two streams in Eastern Oregon (described in Sect. 4). In Sect. 2 we describe the IMS model and the PM, and in Sect. 3 we give a Bayesian version of the PM and add extensions to address the seasonality inherent in the data. In Sect. 4 we compare the Bayesian extensions in an application using radio telemetry data. We make comparisons using Bayesian Information Criterion (BIC) values and examination of 95% posterior intervals. We conclude with a discussion in Sect. 5.

## 2 Existing habitat selection models

Following McCracken et al. (1998), suppose  $m$  animals are tracked and can be observed in any one of  $H$  habitat classes at each of  $T$  sampling occasions. For animal  $i$ , let  $\mathbf{X}_i = (x_{i1}, x_{i2}, \dots, x_{iH})$ , where  $x_{ih}$  denotes the number of times animal  $i$  is observed in habitat  $h = 1, \dots, H$ . Let  $\boldsymbol{\pi} = (\pi_1, \dots, \pi_H)$ , where  $\pi_h$  denotes the probability that an animal is located in habitat  $h$  on any single sighting. Assume that repeated relocations of the same animal are independent events. Then, conditional on  $n_i$ ,  $\mathbf{X}_i$  follows a multinomial distribution, with parameters  $n_i$  and  $\boldsymbol{\pi}$ . By further assuming that different animals make independent habitat selections, the IMS model has a product multinomial likelihood:

$$L(\mathbf{X}_1, \dots, \mathbf{X}_m | \boldsymbol{\pi}) = \prod_{i=1}^m \left\{ n_i! \prod_{h=1}^H \frac{\pi_h^{x_{ih}}}{x_{ih}!} \right\}.$$

In the multinomial logistic parameterization of the IMS model, we can incorporate habitat characteristic information (McCullagh and Nelder 1989; Ramsey and Usner 2003). Taking habitat  $H$  as the reference level, for covariates  $Z_{1h}, \dots, Z_{ph}$ , corresponding to habitat  $h \in \{1, \dots, H-1\}$ ,

$$\log(\pi_h/\pi_H) = \beta_0 + \beta_1(Z_{1h} - Z_{1H}) + \dots + \beta_p(Z_{ph} - Z_{pH}). \quad (1)$$

Following Ramsey and Usner (2003), we define a selection probability ratio (SPR) as the ratio of one HSP to that of a reference habitat. Thus, as shown above,  $\log(\text{SPR})$  is expressed as a linear function of covariates in the multinomial logit model. These covariates might include continuous variables such as the area of each habitat or binary indicators of the presence or absence of a particular characteristic. Differences in areas among habitat classes, or logarithms of ratios of areas, should also be included in the multinomial logit expression as offset variables, as this allows for inclusion of habitat class availability into the analysis (Ramsey and Usner 2003). Further details for the inclusion of availability are given in Sect. 4, specifically in Eqs. 9 and 10 and the discussion that follows.

A common concern in the analysis of radio telemetry data is how to address the assumption of independence for repeat locations of the animals. A common solution is to make a further assumption that the animal relocations are far enough apart in time that they can be considered independent. Ramsey and Usner (2003) offer an alternative model, PM, that allows for the lack of independence inherent in the data by explicitly modeling persistence. Thus, the PM extends the IMS model by relaxing the assumption that repeat relocations of the same animal are independent. Following Ramsey and Usner, assume that relocations in the  $H$  habitat classes form an  $H$ -state Markov chain with transition probability matrix  $T = [p_{jh}]$  for  $j, h = 1, \dots, H$ , where

$$p_{jh} = \begin{cases} 1 - \eta(1 - \pi_h) & : j = h, \\ \eta\pi_h & : j \neq h. \end{cases} \quad (2)$$

Here,  $\eta$  is a measure of persistence with range

$$0 \leq \eta \leq \min_h \left\{ \frac{1}{\pi_h}, \frac{1}{1 - \pi_h} \right\} \quad (3)$$

for  $h = 1, \dots, H$ . If  $\eta = 1$  then the PM reduces to the IMS model, and if  $\eta < 1$ , animals tend to persist in the same habitat from one sighting occasion to the next.

Again, we assume that the relocation history of any one animal is independent of that of the other animals. We define the following quantities for animal  $i$ . Let  $f_{ih}$  be an indicator of animal  $i$ 's initial location in habitat  $h$ ; that is,  $f_{ih} = 1$  if the first time animal  $i$  is located it is in habitat  $h$ ; and  $f_{ih} = 0$  otherwise. Let  $n_{ih}$  denote the number of transitions in which animal  $i$  stays in habitat  $h$  from one relocation to the next (i.e. persists), and let  $v_{ih}$  denote the number of transitions that animal  $i$  makes into habitat  $h$  from any other habitat (i.e. moves). Summing over  $m$  animals, the corresponding sample-based quantities are  $f_h = \sum_{i=1}^m f_{ih}$ ,  $n_h = \sum_{i=1}^m n_{ih}$  and  $v_h = \sum_{i=1}^m v_{ih}$ .

Based on the transition probabilities in Eq. 2, the likelihood for the PM, combining data from all animals, is given by:

$$\begin{aligned} L(\mathbf{X}_1, \dots, \mathbf{X}_m | \boldsymbol{\pi}, \eta) &\propto \prod_{i=1}^m \prod_{h=1}^H \pi_h^{f_{ih}} (\eta \pi_h)^{v_{ih}} (1 - \eta(1 - \pi_h))^{n_{ih}} \\ &= \prod_{h=1}^H \pi_h^{f_h} (\eta \pi_h)^{v_h} (1 - \eta(1 - \pi_h))^{n_h}. \end{aligned} \quad (4)$$

As with the IMS model, the  $\pi_h$ 's are parameterized by means of a multinomial logit link as in Eq. 1. Note that the likelihood can just as easily be expressed for an individual animal.

### 3 Bayesian formulation and extensions

Formulation of the PM, Eq. 4, in the Bayesian framework requires the specification of priors for the habitat parameters,  $\boldsymbol{\beta}$ , and the persistence parameter,  $\eta$ . We find the Bayesian paradigm in this application particularly appealing in that it allows direct probabilistic interpretations of the persistence parameter. Under non-informative priors, the Bayesian results agree with the results of the original PM fit by means of iterative maximum likelihood estimation. Further, the Bayesian parameterization of the PM provides the basis for extensions to accommodate data collected across multiple seasons. We first describe these extensions and then discuss prior distributions for the Bayesian models.

First, consider the case in which the persistence parameter is allowed to vary by season, but the HSP remain fixed through the seasons. Let  $S$  denote the number of seasons for which data are obtained. We modify the PM by constructing  $S$  transition probability matrices, one per season, where each matrix,  $\mathbf{T}_s = [q_{jh}^s]$ , has elements

$$q_{jh}^s = \begin{cases} 1 - \eta_s(1 - \pi_h) & : j = h, \\ \eta_s \pi_h & : j \neq h. \end{cases}$$

Here,  $\eta_s$ , for  $s = 1, 2, \dots, S$ , is a seasonal persistence parameter, and differences in persistence across seasons can be evaluated by examining differences in the  $\eta_s$ 's. As with the PM, there are constraints on  $\eta_s$ :

$$0 \leq \eta_s \leq \min_h \left\{ \frac{1}{\pi_h}, \frac{1}{1 - \pi_h} \right\}.$$

To accommodate the  $S$  transition probability matrices, we define season-specific quantities for each animal,  $f_{ish}$ ,  $n_{ish}$  and  $v_{ish}$  to parallel the quantities  $f_{ih}$ ,  $n_{ih}$  and  $v_{ih}$  defined in Sect. 2. That is,  $f_{ish} = 1$  if the first sighting of animal  $i$  in season  $s$  occurs in habitat  $h$ , and  $f_{ish} = 0$  otherwise. The corresponding seasonal summaries are  $f_{sh} = \sum_{i=1}^m f_{ish}$ ,  $n_{sh} = \sum_{i=1}^m n_{ish}$  and  $v_{sh} = \sum_{i=1}^m v_{ish}$ . Accordingly, the modification to the likelihood in Eq. 4 is:

$$L(\mathbf{X}_1, \dots, \mathbf{X}_m | \boldsymbol{\eta}, \boldsymbol{\pi}) \propto \prod_{s=1}^S \prod_{h=1}^H \pi_h^{f_{sh}} (\eta_s \pi_h)^{v_{sh}} (1 - \eta_s(1 - \pi_h))^{n_{sh}}. \quad (5)$$

We denote this model EXT1. Again, this model is easily written for a single animal.

Next, we assume the persistence parameter to be fixed through seasons, but allow the HSP to change by season. That is, take  $\pi_{sh}$  to be the probability of a sighting in habitat  $h$  during season  $s$ , whereby  $\sum_{h=1}^H \pi_{sh} = 1$  for  $s = 1, \dots, S$ . This extension to the PM also corresponds to  $S$  transition probability matrices  $\mathbf{T}_s^* = [r_{jh}^s]$ , with

$$r_{jh}^s = \begin{cases} 1 - \eta(1 - \pi_{sh}) & : j = h, \\ \eta\pi_{sh} & : j \neq h. \end{cases}$$

The persistence parameter,  $\eta$ , is constrained by all of the HSP:

$$0 \leq \eta \leq \min_{h,s} \left\{ \frac{1}{\pi_{sh}}, \frac{1}{1 - \pi_{sh}} \right\}.$$

Under this extension (EXT2), the likelihood component in Eq. 4 becomes:

$$L(\mathbf{X}_1, \dots, \mathbf{X}_m | \eta, \boldsymbol{\pi}) \propto \prod_{s=1}^S \prod_{h=1}^H \pi_{sh}^{f_{sh}} \eta^{n_h} \pi_{sh}^{n_{sh}} (1 - \eta(1 - \pi_{sh}))^{v_{sh}}. \quad (6)$$

Finally, we combine these two extensions to include both seasonal persistence and seasonal HSP. In this case, the  $S$  transition probability matrices are  $\mathbf{T}_s^{**} = [u_{jh}^s]$ , with

$$u_{jh}^s = \begin{cases} 1 - \eta_s(1 - \pi_{sh}) & : j = h, \\ \eta_s\pi_{sh} & : j \neq h. \end{cases}$$

Now, each  $\eta_s$  has its own constraint, corresponding to the HSP for season  $s$ :

$$0 \leq \eta_s \leq \min_h \left\{ \frac{1}{\pi_{sh}}, \frac{1}{1 - \pi_{sh}} \right\}.$$

The corresponding likelihood component for this model (EXT3) is given by

$$L(\mathbf{X}_1, \dots, \mathbf{X}_m | \boldsymbol{\eta}, \boldsymbol{\pi}) \propto \prod_{s=1}^S \prod_{h=1}^H \pi_{sh}^{f_{sh}} (\eta_s \pi_{sh})^{n_{sh}} (1 - \eta_s(1 - \pi_{sh}))^{v_{sh}}. \quad (7)$$

As in the case of the IMS model and the PM, a multinomial logit parameterization can be incorporated into the likelihood in Eq. 5 by replacing the  $\pi_h$ 's with the expression obtained from solving the specified logit equation, as in Eq. 1. For models EXT2 and EXT3 that incorporate seasonal HSP, we construct a logistic link for each season. Consider  $(Z_{1sh}, \dots, Z_{psh})$  to be habitat and season specific covariates. For instance,  $Z_{jsh}$  might be the area of habitat  $h$  in season  $s$ . For  $s = 1, \dots, S$ , taking  $H$  as the reference habitat in each season, let

$$\log(\pi_{sh}/\pi_{sH}) = \beta_{0s} + \beta_{1s}(Z_{1sh} - Z_{1sH}) + \dots + \beta_{ps}(Z_{psh} - Z_{psH}). \quad (8)$$

Thus, the natural logarithms of seasonal SPRs are now expressed as linear functions of seasonal habitat characteristics, and availability can be incorporated.

### 3.1 Prior distributions

For the Bayesian parameterization of the PM, we specify prior distributions for  $\eta$  and the parameters of the multinomial logit in Eq. 1,  $\boldsymbol{\beta}$ . The constraint on  $\eta$  shown in Eq. 3 allows  $\eta > 1$ ; however, when a degree of persistence is present (i.e., an animal is more likely to be sighted in the habitat in which it was previously sighted than in a different

habitat),  $\eta$  will be less than one. We assume a relatively high degree of persistence is present and that the posterior distribution of  $\eta$  contains only values less than one to restrict  $\eta$  to the interval  $(0, 1)$ . This allows for a non-informative, uniform prior for  $\eta$ . For data with less persistence and a persistence parameter closer to one, or for testing whether the persistence parameter is different from 1, this prior should be changed to allow  $\eta > 1$ . For instance, we might use a uniform  $(0, k)$  prior, for some  $k > 1$ , and maintain the restriction on  $\eta$  using its proposal distribution. We take  $\beta$  independent of  $\eta$  with a diffuse Normal prior with mean zero and variance 400.

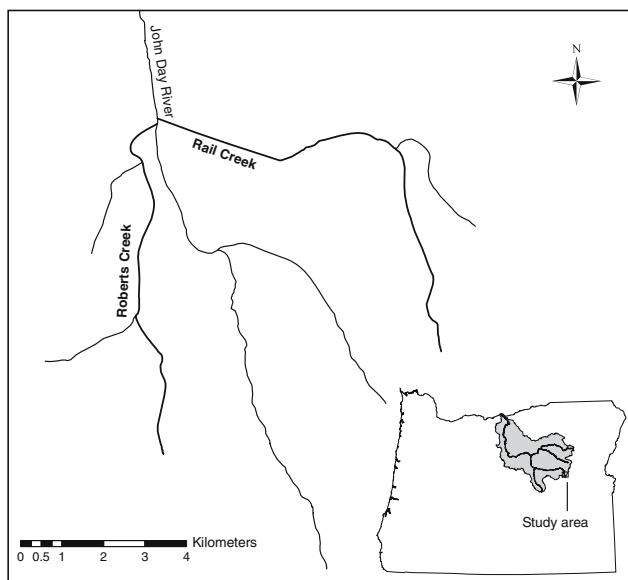
For models EXT1 and EXT3, in which the persistence parameter differs for each season, we use two priors and compare the results. The first, P1, expresses each  $\eta_s$  as an independent uniform;  $\eta_s \sim \text{Beta}(1, 1)$  for  $s = 1, \dots, S$ . In the second, P2, we construct a hierarchical model for the  $\eta_s$ 's, where  $\eta_s \sim \text{Beta}(a, b)$  for  $s = 1, \dots, S$ , and  $\pi(a, b) = \pi(a)\pi(b)$  where  $\pi(a)$  and  $\pi(b)$  are independent diffuse gamma distributions. This second prior allows us to consider annual persistence using our estimate of the posterior quantity  $a/(a + b)$ , the mean of seasonal persistence.

For models EXT2 and EXT3, in which the HSP vary with season, we use a diffuse Normal prior for the multinomial logit parameters,  $\beta$ . We ran all Markov chain Monte Carlo (MCMC) chains for 20,000 iterations, and calculated estimates and posterior intervals after removing the first 1,000 iterations for burn-in. The sample path plots showed good mixing and the chains appeared to converge well within the first 500 iterations of the chain.

#### 4 Application to westslope cutthroat trout data

Westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and other cutthroat trout subspecies have experienced substantial declines from their historical distribution and populations continue to face many anthropogenic threats to their long-term survival (Gresswell 1988; McIntyre and Rieman 1995). In the most recent estimate, over 90% of strong westslope cutthroat trout populations have been relegated to steep, high-elevation, forested headwater basins on publicly owned land, where they generally have found protection from colonization by non-native species and the adverse effects of human activities (Lee et al. 1997). Radio telemetry studies of adult cutthroat trout in headwater basins provide substantial evidence of seasonal movements associated with seasonally changing stream conditions, but there is limited understanding of how adult cutthroat trout habitat use changes seasonally (Schlosser 1995; Northcote 1997). A sixteen-month radio telemetry study in 2000–2001 of westslope cutthroat trout in Rail Creek and Roberts Creek, two headwater tributaries of the John Day River in eastern Oregon, under the auspices of the Oregon Department of Fish and Wildlife and Oregon State University, provides data for describing the seasonal habitat associations and movement patterns of adult westslope cutthroat trout (details in Starcevich 2004; see Fig. 1). It was hypothesized that habitat associations and movement patterns would change seasonally as the habitat needs of the fish changed to accommodate summer feeding, winter refuge from cold stream temperatures and frazil ice, and spring spawning and refuge from high discharge.

Twenty-six trout—9 fish in Rail Creek and 17 in Roberts Creek—were successfully followed across three seasons: winter, spring, and summer. Not all radio-tagged trout were tracked through all seasons as a result of mortality and expelled or expired transmitters. The fish used in our analysis were relocated at least six times in winter (range:



**Fig. 1** Rail and Roberts Creeks in Eastern Oregon

6–19), at least four times in the summer (range: 4–11) and throughout the entire spring season (nine relocations). The fall season was excluded from the analysis due to the short transition period from summer to winter in these headwater basins and the small number of fish tracked through all four seasons. There are weekly (approximately) measurements for each fish with several missing data points representing weeks that individual fish were not relocated. To estimate seasonal habitat availability, the habitat of each creek was inventoried in the winter, spring, and summer. Channel unit type and structural association of pools were among the habitat variables used in the habitat association analysis. For the analysis described in this paper, channel unit types are divided into three mutually exclusive habitat types: (1) pools that are structurally associated with in-stream large wood (ILW), (2) all other pools (OP), and (3) fast water units such as riffles and rapids (FW). Seasonal habitat availability, as measured in the seasonal habitat inventories, is calculated by the surface area of a particular channel unit type divided by the total surface area of the stream and is represented as a percentage. It is assumed that the entire stream is available to each fish, which is thought to be a valid assumption based on the large distances covered by several fish.

Table 1 shows habitat selection counts by season summed across all fish for both Roberts and Rail Creeks. These summaries suggest that the combined habitat use changes with season and that use may be different between the two creeks. Table 2 shows seasonal habitat availability information for both creeks. The slight changes in availability across the year are largely a result of the difference between spring snowmelt-driven high discharge and summer and winter baseflows.

Individual fish exhibit clear persistence in particular habitat classes, and the degree of persistence often changes with season. For example, Fig. 2 shows habitat relocations for one fish from Roberts Creek and one fish from Rail Creek over the three seasons. These two fish appear to be more likely to persist in one habitat type than to move

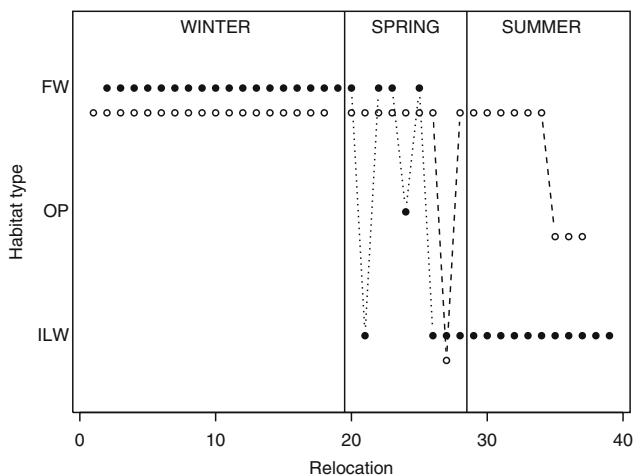
**Table 1** Counts of relocations in Rail and Roberts Creeks by season, according to habitat

	Roberts Creek				Rail Creek		
	ILW	OP	FW		ILW	OP	FW
Winter	35	5	70	Winter	90	47	106
Spring	44	11	23	Spring	71	7	66
Summer	38	24	24	Summer	64	25	33
Total	117	40	117	Total	225	79	205

ILW = in-stream large wood; OP = other pool; FW = fast water

**Table 2** Habitat availability as a percentage of total area for Roberts and Rail Creeks by season

	Roberts Creek				Rail Creek		
	ILW	OP	FW		ILW	OP	FW
Winter	7.5	2.9	89.5	Winter	7.9	2.6	89.6
Spring	8.0	2.2	89.8	Spring	8.5	3.3	88.2
Summer	7.5	2.9	89.5	Summer	7.9	2.6	89.6

**Fig. 2** Radio telemetry data for fish X (solid circles) from Roberts Creek and fish Y (open circles) from Rail Creek. Vertical lines indicate end of Winter and Spring seasons, respectively from left to right

to a different habitat type. Seasonal cutoffs were determined by means of a priori criteria based on stream temperature, discharge thresholds, and observational criteria such as spawning of westslope cutthroat trout and sympatric fish species. Using these criteria resulted in a winter season that was nearly twice as long as spring and summer. Table 3 shows the percentage of persists (regardless of habitat type) out of the total number of relocations of all fish per season for both Rail Creek and Roberts Creek. It is clear that there is a strong degree of persistence that does vary with both season and stream.



**Table 3** Persistence expressed as percentage of the total number of relocations per season for Roberts and Rail Creeks (percent persists + percent moves = 100)

	Winter	Spring	Summer
Roberts	84.58	62.99	76.19
Rail	80.39	50.00	63.75

Following Ramsey and Usner (2003), we offset the multinomial logit parameterizations by the logarithm of the availability ratio (AR), so that

$$\log(\pi_h/\pi_H) = \beta_h + (\log(A_h) - \log(A_H)) \quad (9)$$

and

$$\log(\pi_{sh}/\pi_{sH}) = \beta_{sh} + (\log(A_h) - \log(A_H)) \quad (10)$$

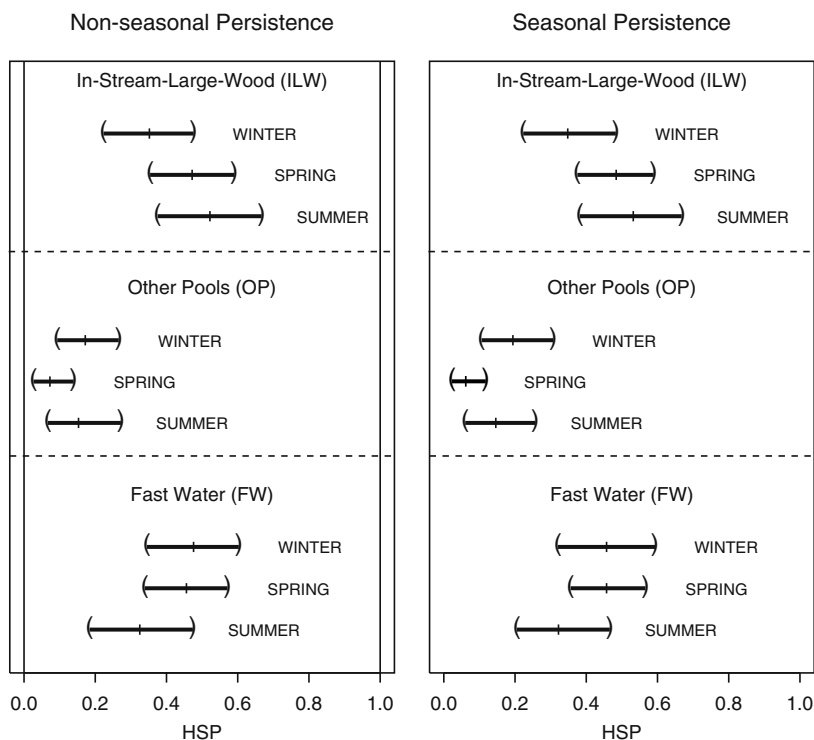
define our specific parameterizations of Eqs. 1 and 8, respectively. The AR is defined by the ratio of  $A_h$ , denoting the availability of habitat  $h = 1, \dots, H - 1$ , and  $A_H$ , denoting the availability of habitat  $H$ . The inclusion of availability is an integral part of our analysis as it allows for investigating use of a habitat class relative to its availability. This parameterization allows us to exploit the fact that the multinomial logit model describes the  $\log(\text{SPR})$  to test whether SPRs are significantly smaller than their respective ARs, and to obtain estimates and uncertainty intervals for the ratios,  $\text{SPR}/\text{AR}$ . For more detail regarding this parameterization see Ramsey and Usner (2003) and Usner (2000).

We performed the analyses using the combined data from all fish. However, in the presence of obvious heterogeneity among animals, the models should be fit to each animal individually (Manly et al. 2002). Our Bayesian models are estimated by means of MCMC methods, implemented in R (R Development Core Team 2004). Complete conditional distributions are shown in the Appendix. Table 4 shows estimates of persistence for both Roberts and Rail Creeks under the PM, EXT1, EXT2 and EXT3. For both creeks, EXT2 and EXT3 clearly demonstrate seasonal differences in persistence; specifically, animals show more persistence in the winter and summer than in the spring. This is consistent with the hypothesized seasonal changes in westslope cutthroat trout behavior, characterized by summer feeding, winter refuge, and spring spawning.

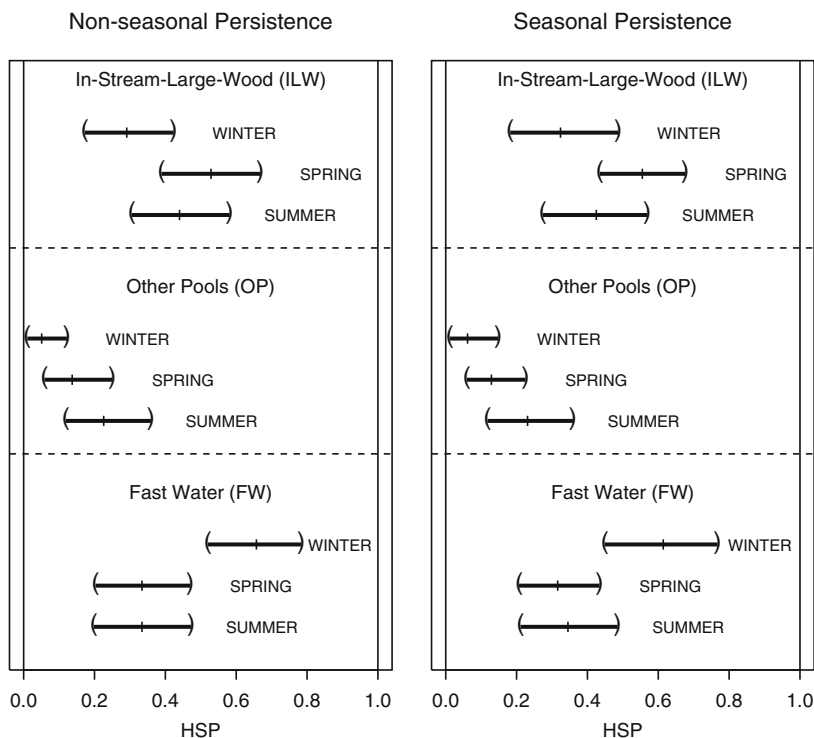
The results in Table 4 for EXT1 and EXT3 are based on our non-informative prior, P1. The estimates of the seasonal persistence parameters under P2 are identical, and we obtain the additional estimate of annual persistence. For example, under EXT3 for Roberts Creek, annual persistence is estimated to be 0.468 (0.122). Notice the large standard deviation relative to those of the seasonal estimates. 95% posterior intervals are constructed by means of the common method of obtaining the 0.025 and 0.975 quantiles from the samples of the posterior distribution obtained through MCMC (Gelman et al. 2004). We are comfortable using this simpler, more interpretable method over that of calculating highest probability density intervals because of the unimodal and fairly symmetric nature of the posterior distributions. The 95% posterior intervals for annual persistence span the range covered by the three seasonal intervals, providing little precision in estimating an overall persistence parameter and pointing to the advantage of using the seasonal estimates.

**Table 4** Estimates of persistence—posterior means (sd)—for the PM and EXT1, EXT2, and EXT3

	PM	EXT1	EXT2	EXT3
<i>Roberts Creek</i>				
Persistence	0.397 (0.033)	—	0.402 (0.033)	—
Winter	—	0.251 (0.038)	—	0.248 (0.038)
Spring	—	0.660 (0.078)	—	0.685 (0.075)
Summer	—	0.379 (0.062)	—	0.397 (0.069)
<i>Rail Creek</i>				
Persistence	0.561(0.048)	—	0.605 (0.051)	—
Winter	—	0.345 (0.071)	—	0.403 (0.081)
Spring	—	0.811 (0.089)	—	0.824 (0.087)
Summer	—	0.551 (0.077)	—	0.555 (0.079)

**Fig. 3** Habitat selection probabilities (HSP) for Roberts Creek using models EXT2 and EXT3

While the seasonality of persistence stands out, the HSP do not tend to change by season for Roberts Creek. Fig. 3 shows 95% posterior intervals for the HSP estimated from the data at Roberts Creek for EXT2 and EXT3. There is substantial overlap of these seasonal intervals within habitats. In contrast, Fig. 4 shows 95% posterior intervals for the HSP estimated from Rail Creek data under EXT2 and EXT3, and these do tend to be slightly different by season. The HSP estimates and intervals, however, describe frequency of use without regard to the relative availability of habitats.



**Fig. 4** Habitat selection probabilities (HSP) for Rail Creek using models EXT2 and EXT3

**Table 5** Selection probability ratio to area ratio ratios (95% posterior intervals) for Roberts and Rail Creeks under EXT1

SPR/AR	EXT1
Roberts Creek	
ILW/FW	12.76 (9.12,17.60)
OP/FW	9.60 (5.71,15.07)
Rail Creek	
ILW/FW	12.84 (8.61,18.44)
OP/FW	10.69 (6.09,17.58)

Our Bayesian parameterizations allow for straightforward estimation of the SPR/AR ratios to account for relative availability in habitat comparisons. These are easily obtained as functions of the posterior parameters estimated using MCMC. Table 5 displays SPR/AR ratios for EXT1. Fast water (FW) is used as the reference habitat, resulting in two SPR/AR estimates for each model. For both creeks, the SPRs for in-stream-large-wood (ILW) and other pools (OP) are significantly larger than their respective proportions available, as the 95% posterior intervals for the SPR/AR ratios clearly do not cover one. This is evidence that the pools are used disproportionately to their availability in the streams. For example, it is estimated for Roberts

**Table 6** BIC model comparisons for Roberts Creek and Rail Creek

	persistence	Habitat selection probabilities	BIC Roberts	BIC Rail
PM	Non-seasonal	Non-seasonal	742.6	482.2
EXT1	Seasonal	Non-seasonal	711.6	467.8
EXT2	Non-Seasonal	Seasonal	751.2	479.4
EXT3	Seasonal	Seasonal	717.0	469.2

Creek that the SPR,  $\pi_{ILW}/\pi_{FW}$ , is 12.76 times that of the ratio of their respective areas,  $\text{Area}_{ILW}/\text{Area}_{FW}$ , with a 95% posterior interval ranged from 9.12 to 17.60 times.

To compare the PM and its three extensions, we calculated the BIC (Schwarz 1978) for each. These values are shown in Table 6. Notice that even with the penalty for more parameters, EXT1 does better than the PM and the EXT3 does better than EXT2 (though admittedly not by much), as a result of the evidence of seasonal persistence. For both creeks, EXT1, the seasonal persistence and non-seasonal HSP model, appears best under the BIC selection criterion.

## 5 Discussion

Most existing methods for analyzing radio telemetry data have ignored the multiple sources of statistical dependence in the data. The analysis presented here provides one method for relaxing the assumption that repeat relocations of the same animal represent independent habitat selections—by incorporating seasonal persistence and seasonal habitat selection probabilities. There are several advantages to the Bayesian model over the original PM described by Ramsey and Usner (2003), including the ease of obtaining variability estimates for the parameters and functions of the parameters; these are byproducts of the MCMC procedure. Furthermore, our variability estimates and intervals are sample size specific and not based on asymptotic properties of maximum likelihood estimates, in contrast to those from the original PM.

The persistence parameter itself provides biologically interesting and meaningful information about habitat use. It gives a summary measure related to the relative amount of time an animal continually stays in a particular habitat before moving to a different habitat for one or more relocations. For example, westslope cutthroat trout showed seasonal differences in persistence with the greatest persistence in the winter. This supports the hypothesized seasonal changes in westslope cutthroat trout behavior. Fish are expected to be less active and mobile in the winter than they are at other times, as they seek refuge from harsh stream conditions (Starcevich 2004). Further extensions to the PM could combine data from multiple sample sites, such as the two streams in this analysis, with a hierarchical approach.

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## Appendix

### Complete conditional distributions

We give the complete conditional distributions for the most general model, EXT3, whose likelihood is reproduced here:

$$L(\mathbf{X}_1, \dots, \mathbf{X}_m | \boldsymbol{\eta}, \boldsymbol{\beta}) \propto \prod_{s=1}^S \prod_{h=1}^H \pi_{sh}^{f_{sh}} (\eta_s \pi_{sh})^{n_{sh}} (1 - \eta_s (1 - \pi_{sh}))^{v_{sh}}.$$

We also assume

$$p(\boldsymbol{\eta}, \boldsymbol{\beta}) = p(\boldsymbol{\eta})p(\boldsymbol{\beta}).$$

The complete conditional distribution of  $\eta_s$  given the data and the remaining parameters is given by

$$p(\eta_s | ---) \propto p(\eta_s) \eta_s^{n_s} \left\{ \prod_{h=1}^H (1 - \eta_s (1 - \pi_{sh})) \right\}^{v_{sh}},$$

where  $n_s = \sum_{h=1}^H n_{sh}$ , and where,

$$\pi_{sh} = \frac{e^{Q_{sh}}}{1 + e^{Q_{s1}} + \dots + e^{Q_{sH-1}}}$$

and

$$\pi_{sH} = \frac{1}{1 + e^{Q_{s1}} + \dots + e^{Q_{sH-1}}}.$$

For our examples,

$$Q_{sh} = \beta_{sh} + \log(A_{sh}/A_{sH}),$$

where  $A_{sh}$  denotes the availability of habitat  $h$  in season  $s$ .

The complete conditional distribution of  $\beta_{sh}$  given the data and remaining parameters, for  $s = 1, \dots, S$  and  $h = 1, \dots, H$ , is

$$p(\beta_{sh} | ---) \propto \pi_{sh}^{f_{sh} + n_{sh}} (1 - \eta_s (1 - \pi_{sh}))^{v_{sh}} p(\beta_{sh}).$$

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